The Reproductive Cycle of

Lodgepole Pine

Province of British Columbia
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PREFACE

British Columbia has 25 native conifer species, of which 15 are commercially important and scheduled for reforestation. Tree improvement programs for four of these species are now under way and programs for several other species are planned. A necessary prerequisite for extensive reforestation and tree improvement programs is a complete understanding of the reproductive cycle of each species.

Until 1970, Douglas-fir was the only native species for which the complete reproductive cycle was known. Since that time, studies of the reproductive cycles have been completed for 13 of the other commercially important conifers. These studies include descriptions of vegetative bud and shoot development as they relate to cone initiation, the time and method of cone initiation, predormant and postdormant cone-bud development, pollen development, pollination, and embryo and seed development. Although these studies provide essential details of the reproductive cycles, a more general description of all aspects of the reproductive cycle of a particular species is frequently requested.

This request has resulted in a series of short books concerning the reproductive cycles of several conifers. Serving as ready references for foresters and others concerned with seed production and tree improvement, these books will explain the complete reproductive cycle; provide useful guidelines for cone induction studies; assist in forecasting pollen and seed production; enable more effective pollination; and provide some clues to the causes of poor seed production. In addition, such information should be useful to students of forestry and biology at universities, technical schools and high schools.

This book, *The Reproductive Cycle of Lodgepole Pine*, is not meant to include a complete literature review. Only the most pertinent and accessible references are cited and listed, providing a source for numerous related reports.

ACKNOWLEDGEMENTS

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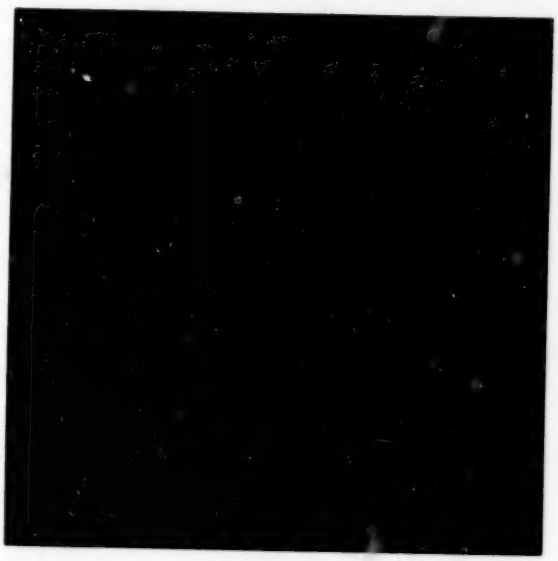
The Reproductive Cycle of Lodgepole Pine



Introduction

Lodgepole pine (*Pinus contorta* Dougl.) is a member of the Pinaceae, the largest family of conifers. There is no general agreement on the number of species of *Pinus*, with estimates ranging from 66 to 120 species. The most recent and complete review of the genus lists 94 species (Critchfield and Little 1966). The discrepancy in the number of species is a result of the wide distribution of the genus over much of the northern hemisphere. Many species in various geographic locations often appear to belong to *Pinus*.

Lodgepole pine is one of the most familiar, widespread, and important species of pi in North America. It extends from the Mackenzie District of the Yukon in Canada, south to southern Colorado and northern Baja, California (Fig. 1). Within this distribution it grows at a wider range of elevations than any other conifer, occurring just above sea level along the Pacific coast, up to approximately 3400 m in the southern Sierra Nevada and Rocky Mountains (Fowells (compiler) 1965). Because of its wide distribution, two to four geographical varieties or subspecies are commonly recognized (Pfister and Daubenmire 1975). *Pinus contorta* var. *contorta*, or shore pine, occurs along the Pacific coast and is the most distinct in form, being generally short and crooked with a flattened crown and non-serotinous cones. *Pinus contorta* var. *latifolia*, to which the common name of lodgepole pine is usually applied, is distributed throughout the interior regions. These trees are generally tall and straight, with a narrow crown, and usually have serotinous cones. Both *Pinus contorta* var. *murrayana*, a tree of the Cascade and Sierra Nevada mountains, and *Pinus contorta* spp. *bolanderi*, from the Mendocino white plains in California, may be considered as separate interior varieties or subspecies, or may be combined with *Pinus contorta* var. *latifolia*. Distinction between the latter three subspecies is based primarily on quantitative morphological and behavioural traits. Where the ranges of the varieties are sympatric, they interbreed freely. Along the northeastern limits of lodgepole pine distribution, its range is sympatric with its closest relative, *Pinus banksiana* Lamb., and they hybridize freely (Illingworth 1971).

The wide distribution and variation of the species make it difficult to describe the reproductive phenology, or time sequence, of the reproductive cycle. The occurrence of a particular event may vary by more than one month in individuals at extremes of its distribution. Consequently, the phenology given is that of *Pinus contorta* var. *latifolia* growing at moderate elevations in approximately the centre of its distribution in central British Columbia. Even though the phenology will vary with geographical distribution, the sequence and details of reproductive development remain the same and a single general description of the reproductive cycle is valid (Fig. 2).

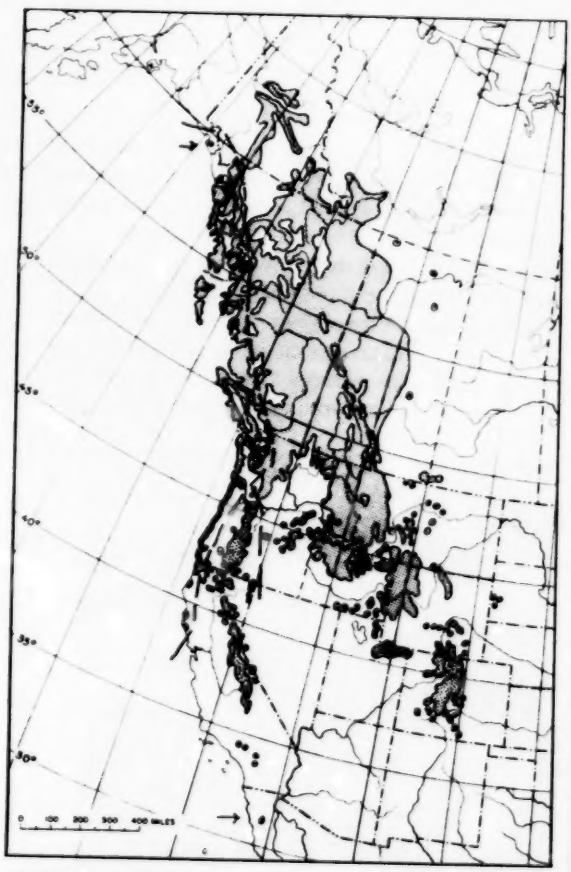


FIGURE 1. Distribution of *Pinus contorta*. Dashed lines show approximate boundaries of varieties. (Reproduced from Little, 1971.)

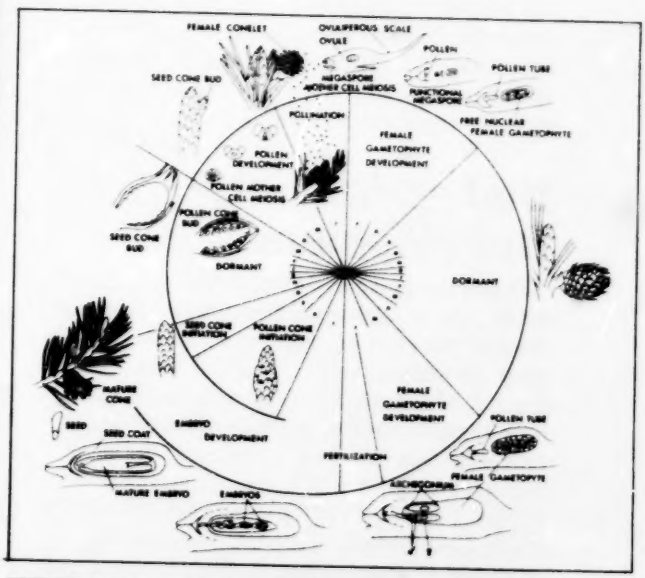


FIGURE 2. The reproductive cycle of *Pinus contorta* extends over 26 months, from cone initiation to seed maturity. Inside the spiral represents male development; outside, female and embryo development. The centre of the spiral is divided into months.

The wide distribution of lodgepole pine, the predominance of the species in many regions, and its value as a source of timber products make it one of the most extensively harvested forest trees in the west. Its uses include interior panelling, exterior trim, particle board, posts, poles, framing material for light construction, and many specialty items. As well, it is used extensively for pulp and paper. Its value is immeasurable as protective cover for watersheds; as wildlife habitat; as a major and aesthetically pleasing component of the environment for recreation; and as an essential element in the long-term maintenance of the local environment (Baumgartner (editor) 1975).

Lodgepole pine is considered to be a fire, or "pioneer", species, quick to occupy a site where natural or man-caused disturbances have created a condition of full sunlight. It is characterized by low shade tolerance, rapid growth in young trees, slow growth in older trees, and the ability to grow on almost any forest soil. Lodgepole pine produces large quantities of seed, and good seed crops occur every one to three years. Serotinous cones of the interior variety require high temperature to release the seeds. This often follows fire, leading to the rapid establishment of uniform dense stands that often stagnate later when trees are still quite small.

The wide distribution, diversity, utility, and economic importance of lodgepole pine make it a valuable species for reforestation. Because extensive reforestation requires a constant supply of high-quality, economical seed, tree improvement programs have begun and seed orchards established. Sustained efforts in the future will require a thorough understanding of the complete reproductive cycle of this species, including the important events during the 26 months from the onset of cone initiation in the summer and fall, through pollination the following spring, to fertilization and embryo development the year following pollination (Fig. 2).

Bud and Shoot Development

During the spring and summer, lodgepole pine forms buds, or telescoped shoots, which contain all of the structures that will be found on the elongated shoot the following year (Owens and Molder 1975) (Figs. 3, 5*F*). At the tip of each bud, concealed beneath the bud scales, is a dome-shaped mass of embryonic cells called the "shoot apex" or "apical meristem" (Figs. 4, 5*A*). In the spring, when dormancy ends, cells of the apical meristem begin to divide. Cells throughout the long-shoot bud below divide and elongate, causing the bud to expand, and forming a vegetative shoot. Elongation is most

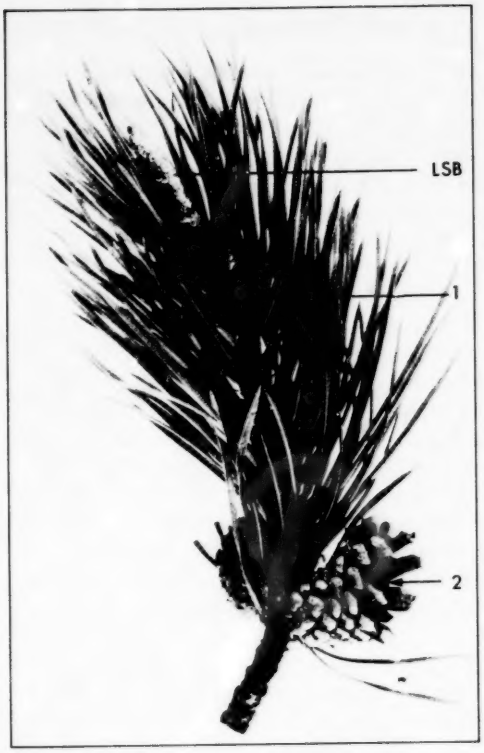


FIGURE 3. A dormant monocyclic long shoot with the distal long-shoot bud (LSB), first-year seed-cones (1), and mature (second-year) seed cones (2). (X 0.5)

extensive first at the base of the long-shoot bud, but the process moves upward along the bud, wavelike. The base of the new shoot completes elongation first, followed by the distal region. The two needle primordia on each of the many short shoots elongate and push out between the scales, or "cataphylls", which enclose the long-shoot bud. Both long-shoot extension growth and needle-elongation growth are completed in early summer. The rate of growth follows a sigmoid pattern that is generally increased

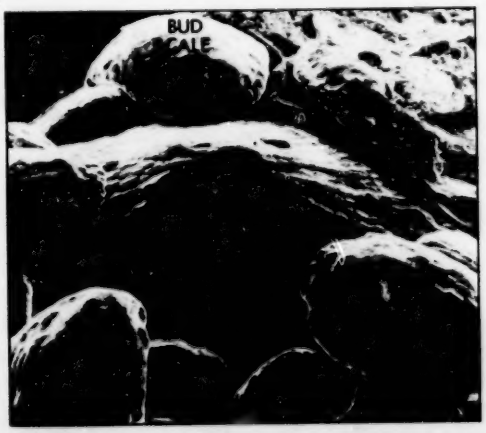


FIGURE 4. A scanning electron micrograph of a dormant long-shoot bud apical meristem partly covered by bud scales. (X 200)

by warm temperatures and decreased by cooler temperatures.

During long-shoot extension growth, the apical meristem, covered by bud scales (Fig. 5*A*), is carried up along with the tip of each terminal or lateral branch, and each apical meristem initiates a new series of cataphylls (Figs. 5*B*-*F*). The first cataphylls begin slowly just after dormancy ends (Fig. 5*B*), and they develop into small, sterile scales at the base of the new long-shoot bud. They begin more rapidly during the following two or three months (Figs. 5*C*, *D*). Soon after each cataphyll is initiated, a small lateral meristem appears in the axil of the cataphyll, that is, just above the juncture of the cataphyll and the bud axis (Fig. 5*C*). Each axillary meristem then initiates several bud scales that enclose and protect it. This process continues until mid-summer, at which time the rate of initiation of lateral meristems in the axils of cataphylls decreases (Figs. 5*D*, *E*). Several of these late cataphylls initiate no axillary meristems ,and remain sterile like the first ones initiated (Fig. 5*E*). The last cataphylls begun in the late summer and early fall are sterile and function as bud scales that enclose and protect the terminal apical meristem (Figs. 5*A*, *F*).

All of the axillary meristems are initiated in the same manner and develop their own protective bud scales. About mid-summer, when the subtending shoot is almost fully elongated and its new terminal long-shoot bud has initiated most of its cataphylls, axillary meristems begin to differentiate (Fig. 5*D*). First are the basal axillary meristems, which differentiate — usually fully before dormancy — into

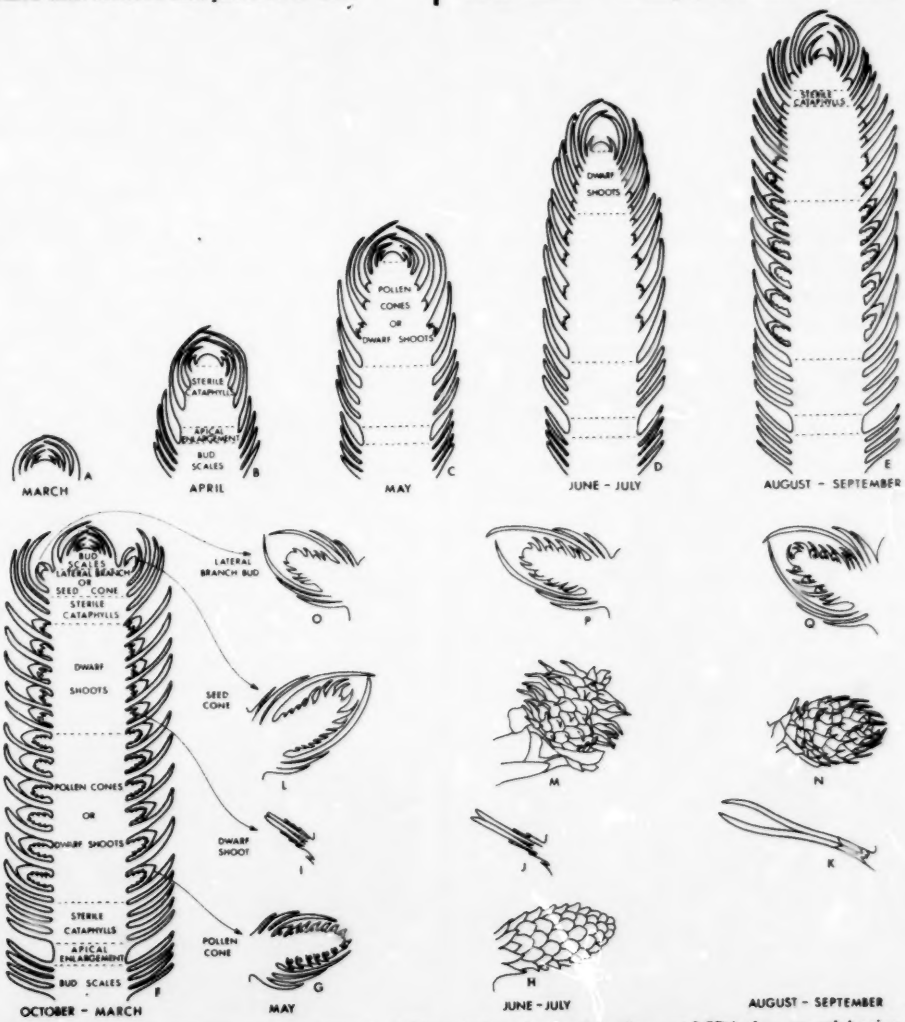


FIGURE 5. Long-shoot bud (LSB) structure and development. *A*. The apical meristem of the dormant LSB before growth begins. *B*. When the LSB begins growth the apex initiates cataphylls. *C*. Cataphylls continue to be initiated and axillary buds begin. *D*, *E*. Axillary buds at the base of the LSB begin to differentiate into pollen cones, or dwarf short shoots, and the rate of cataphyll initiation slows. *F*. Dormant LSB with differentiated basal pollen cones, or short shoots, more distal short shoots, and lateral branch buds, or seed-cone buds. The apex is enclosed by sterile cataphylls. Normally, pollen-cone and seed-cone buds are not formed in the same LSB. *G* - *Q*. Development of the axillary buds after dormancy as the LSB is elongating. The months show the approximate time of development. *G*, *H*. Pollen cone development. *I* - *K*. Short-shoot and needle development. *L* - *N*. Seed-cone development. *O* - *Q*. Lateral branch bud development follows the same sequence as the terminal apical meristem (*A* - *F*).

either pollen-cone buds or short-shoot buds. Next are the distal axillary meristems which may begin to differentiate into seed-cone buds or long-shoot buds, although this development is halted by winter dormancy before it progresses very far (Fig. 5*F*). Pollen-cone buds initiate all of their microsporophylls (Fig. 5*F*), in which pollen will form after dormancy (Figs. 5G, H). Short shoots each initiate two embryonic leaves (Fig. 5*F*) that will elongate after dormancy (Figs. 5*I-K*). Seed-cone buds initiate approximately half of their bracts before dormancy (Fig. 5F), and complete development after dormancy (Figs. 5*L-N*). Lateral branch buds initiate a series of protective bud scales before dormancy (Fig. 5*F*), but after dormancy they mimic the complex series of development as just described for the terminal long-shoot bud (Figs. 5*O-Q*).

Monocyclic and Polycyclic Buds

The development described above and shown in Figure 5 forms a "monocyclic" long-shoot bud, that is, only one sequence of cataphylls and axillary buds (Fig. 3). If two or more sequences ending in lateral branch or seed-cone bud initiation are formed during one growing season (Fig. 6), the result is a "polycyclic" long-shoot bud (Lanner and Van Den Berg 1975). In lodgepole pine it is seldom that more than two or three sequences form. The second and third sequences are shorter than the first because they form late in the growing season. Each sequence is separated by sterile cataphylls and below these a whorl of seed-cone buds and/or lateral branch buds may occur. Seed-cone buds or lateral branch buds that are initiated in the first sequence of a polycyclic long-shoot bud develop more completely than do those in subsequent sequences. That is, the basal seed-cone buds may have initiated nearly all of their bracts (Fig. 5*L*), and lateral branch buds may have initiated many cataphylls and differentiated their axillary short shoots (Fig. 5*Q*) before dormancy.

Although all of the factors that cause buds to become monocyclic or polycyclic are not known, it is known that the vigorous branches in upper regions of the crown are more likely to form polycyclic buds than are the less vigorous branches in lower regions, which usually produce only monocyclic buds. Also known is that some provenances are characterized by a predominance of one or the other bud type. Lodgepole pine, for example, grown out of its natural range, may change from predominantly one type to the other. In general, however, polycyclic bud formations appear to be induced by a prolonged growing season.

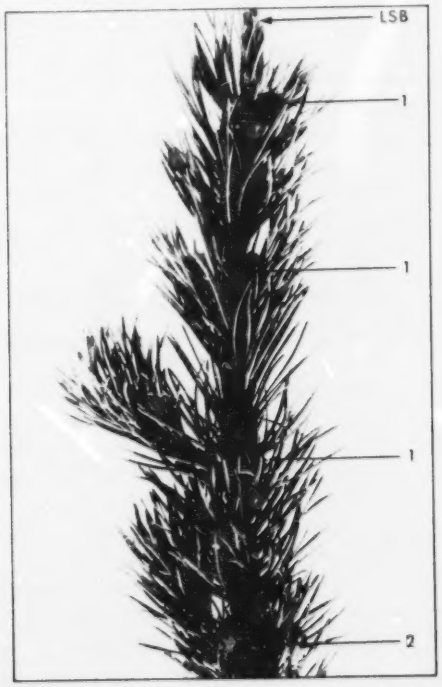


FIGURE 6. A polycyclic long shoot showing the second-year cone (2), and above that three series of axillary shoots. Each series terminates in one or more first-year seed cones (1), and finally a long-shoot bud (LSB) at the distal end. (X 1.5)

Differentiation of Different Bud Types

Axillary primordia may differentiate into short-shoot, long-shoot, pollen-cone, or seed-cone buds (Owens and Molder 1975) (Fig. 5*F*). The pathway, though, along which an axillary primordium may develop, is limited by its time of initiation, position in the long-shoot bud, the position of the long-shoot bud in the tree, and the age and growing conditions of the tree.

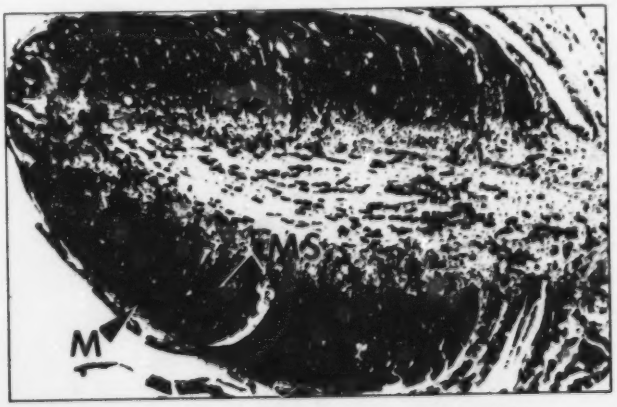


FIGURE 7. A median section through a dormant pollen-cone bud showing microsporophylls (M) each with two microsporangia (MS) which contain sporogenous cells. (X 30)

FIGURE 8. A median section through a dormant short-shoot bud showing the two large leaf primordia and the bud scales. (X 70)

An axillary primordium, for example, initiated at the base of a long-shoot bud in the lower regions of the crown of a reproductively mature tree, will likely develop into a pollen-cone bud (Fig. 7) under some conditions, or into a short-shoot bud (Fig. 8). On the other hand, an axillary primordium initiated in the

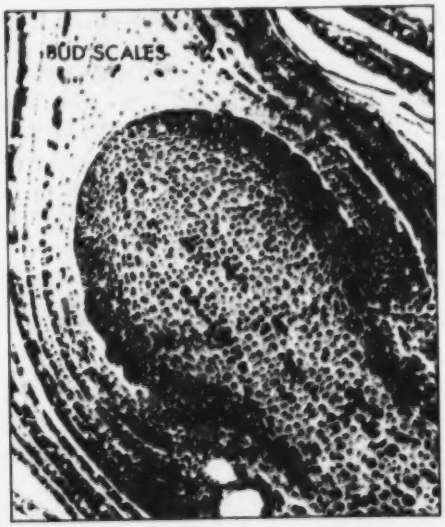


FIGURE 9. A median section through a dormant seed-cone bud showing bract primordia and bud scales. (X 70)

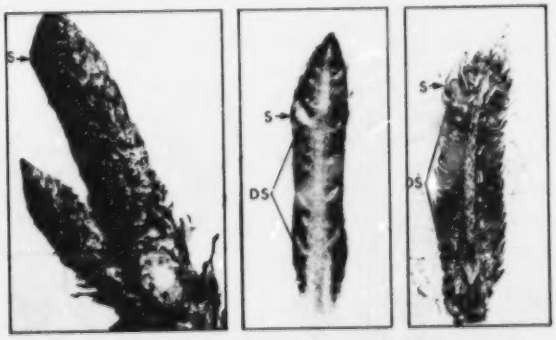
distal part of a long-shoot bud in the upper regions of the crown of a reproductively mature tree will likely develop into a seed-cone bud (Fig. 9) under some conditions, or into a vegetative long-shoot bud (Fig. 10).

FIGURE 10. A median section through a dormant lateral branch bud showing the large apical meristem enclosed by bud scales. (X 150)

Identification of Buds

It is often desirable to estimate the abundance of pollen cones and seed cones that will be available for pollination. This is more difficult in pines than in many other conifers, although estimates can be made by examining the shape of the long-shoot buds, or by dissecting sample long-shoot buds.

During winter a long-shoot bud that usually bears seed-cone buds will appear to swell at the tip on one or more sides (Fig. 11). Each swelling is caused by a seed-cone bud (Figs. 12, 13) rather than a lateral

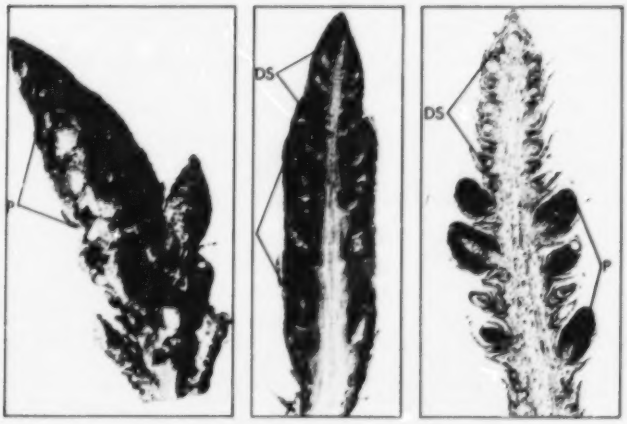


FIGURES 11-13. Dormant long-shoot buds (LSB) bearing seed cone buds. (X 5) FIGURE 11. Whole LSB showing the lateral swelling caused by a large seed-cone bud (S) covered by the cataphylls. FIGURE 12. A LSB sliced down the centre showing seed-cone and short-shoot (DS) buds. FIGURE 13. A median section through a LSB showing seed-cone and short-shoot buds.

branch bud, which is generally smaller.

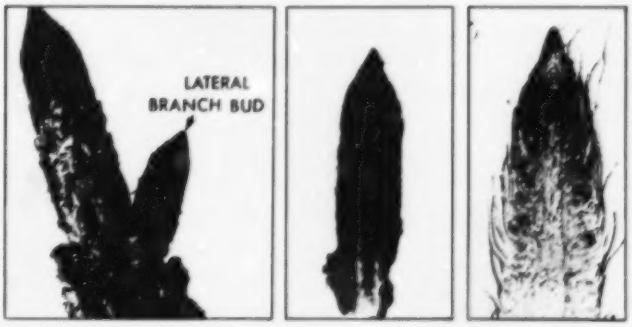
In the fall or winter a long-shoot bud that usually bears pollen-cone buds will appear to swell at the base (Fig. 14). This swelling is caused by several pollen-cone buds which are larger than the short-shoot buds (Figs. 15, 16). A long shoot bud that bears no cone buds usually lacks prominent swellings (Figs. 17-19).

Careful lengthwise slicing of the long-shoot buds will reveal large, white seed-cone buds and pollen-cone buds (Figs. 12, 15), both of which are absent in long-shoot buds that lack cone buds (Fig. 18). Counts of the proportion of long-shoot buds with swellings at the tip or base (or both) will give an estimate of the proportion of branches that will bear seed-cone buds and pollen-cone buds the following spring.



FIGURES 14-16. Dormant long-shoot buds (LSB) bearing pollen-cone buds. (X 5) FIGURE 14. Whole LSB showing swollen base caused by large pollen-cone buds (P) covered by cataphylls. FIGURE 15. A LSB sliced down the centre showing pollen-cone and short-shoot (DS) buds. FIGURE 16. A median section through a LSB showing pollen-cone and short-shoot buds.

Estimates of cone-bud numbers are easier and more accurate if made early in the spring when cone buds begin to enlarge and the swellings become more prominent on the long-shoot bud. Estimates of seed-cone crops that may result from these cone buds 15 months after pollination (Fig. 2) are more tenuous because many factors can cause seed cones to abort during that time. The only conclusion one can make is that if few or no cone buds are present, the cone crop will be small or nil; and if many cone buds are present, there will likely be a good cone crop.



FIGURES 17-19. Dormant long-shoot buds (LSB) bearing no cone buds. (X 5) FIGURE 17. Whole LSB without distinct swellings and a lateral branch bud which was initiated the year before. FIGURE 18. A LSB sliced down the centre showing only short-shoot buds. FIGURE 19. A median section through a LSB showing only short-shoot buds.

Enhancing Cone-Bud Differentiation

The abundance of cone-bud differentiation and, consequently, cone production one year later, is less cyclic in lodgepole pine and some other pines, than in many other conifers. The physiological processes that control the differentiation of axillary primordia into any of the four axillary bud types are poorly understood in

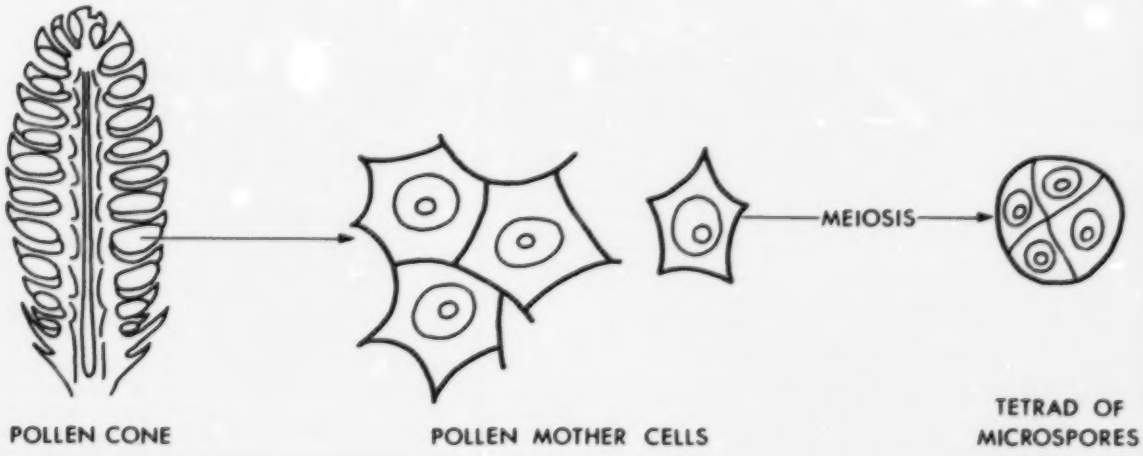


FIGURE 20. Pollen development. The body cell divides to form the two male gametes.

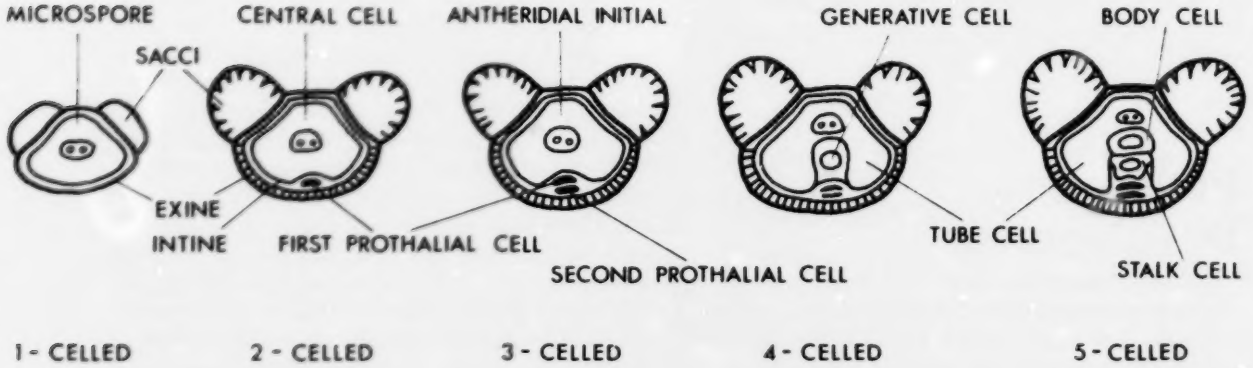
pines (Lee 1979). Several environmental factors, however, are known to promote cone-bud differentiation. These include high temperatures, high amounts of sunshine, and low rainfall, all of which may produce stress, thereby reducing vegetative growth during the summer and fall when cone buds are differentiating (Puritch 1972). These stress conditions promote cone-bud—rather than vegetative-bud — differentiation. As well, abundant rainfall, which promotes vegetative growth in the spring when cataphylls and axillary primordia are being initiated, can promote cone-bud differentiation by increasing the number of cataphylls that might bear axillary cone buds. These factors, plus increased soil fertility, can increase the number of cone buds that differentiate in pines. Consequently, one of the most successful ways to stimulate cone initiation (or "flowering") in natural stands of pine is to remove competition by thinning.

Many specific methods of cone induction have been tried in pines (Lee 1979). Application of nitrogenous fertilizers has promoted female flowering in several pines. Nitrate fertilization of lodgepole pine, for example, promotes female flowering but not male flowering. Stem or branch girdling and strangulation have promoted flowering in many pines, by interfering with the downward movement of food and increasing the carbohydrate content above the constriction. Generally, the greater the interference, the greater the promotion of flowering.

Branch pruning in pine has promoted male and female flowering by increasing the number of branches and, therefore, the number of axillary buds. Branch pruning can also increase branch vigour, which is related to the type of cone induced in pines. Increased branch vigour promotes female cones; decreased branch vigour promotes male cones. Treatments that limit root growth, and consequently water uptake, such as root pruning, root restriction, and transplanting, have increased flowering in some pines, presumably by simulating drought conditions. Many of these treatments result in some degree of permanent injury to the trees. Other injuries that may increase flowering can occur through frost, logging operations, defoliation and disease (Lee 1979).

In recent years plant-growth regulators (hormones) have been used to induce or enhance flowering in conifers (Pharis *et al.* 1975). Early studies used gibberellin A_3 (GA_3) which induced flowering in some species of the Cupressaceae and Taxodiaceae, but not in the Pinaceae. More recently the less polar gibberellins (GA_4, GA_5, GA_7, and GA_9) have been used to induce flowering in several species of the Pinaceae, including lodgepole pine. Other growth regulators, such as auxins, have given conflicting, and often negative, results. Growth regulators have been applied to conifers as foliar sprays or soil drench, or injected or fed into the xylem of the tree by various methods. Such applications have given best results when used in conjunction with other flower-promoting treatments, such as fertilizer, girdling, and water stress.

Lodgepole pine grows rapidly during its juvenile phase of growth, which lasts from four to 10 years for most provenances. During this time, flowering begins in a tree. Seed cones are formed first, followed by pollen cones, often several years later. Flowering in juvenile lodgepole pine has been induced by foliar-spray applications of GA_4 and GA_7 combinations (Wheeler *et al.* 1980). To obtain female flowering trees were sprayed with 500 mg of GA_4 and GA_7 (obtained in 30:70 proportions) plus 25 mg of napthalene acetic acid (NAA) per litre of solvent. The solvent consisted of 95% ethanol (80 ml), distilled water (20 ml), and AROMOX-C cationic detergent (0.1%), included to promote penetration into the foliage. Trees were sprayed once per week for approximately 11 weeks during the period of cone-bud differentiation (Fig. 2). (A spraying should last only



until the wet foliage begins to drip.)

Male flowering has been obtained through the use of a similar foliar spray in combination with girdling at the time of pollen-cone differentiation (Fig. 2). Various injection techniques used successfully in some other members of the Pinaceae have been less successful in pines, possibly because of excessive resin formation at the injection point.

Photoperiod, the relative length of the dark and light period during the 24-hour day, can influence flowering in pines under natural or greenhouse conditions. In conifers studied under natural conditions, shoot elongation slows and then stops as daylengths become shorter. It is believed that the end of shoot elongation and the setting of a bud is a necessary prerequisite to cone bud differentiation. Lodgepole pine grown under continuous light in a greenhouse for six months grew larger and became reproductive at an earlier age than did lodgepole pine grown under natural photoperiods (Wheeler *et al.* 1982). In the future, manipulation of photoperiod-like growth regulator applications can become important cultural treatments for cone induction in juvenile lodgepole pine trees.

Treatments that promote flowering in pine do not seem to increase the number of axillary primordia that could differentiate into cone buds. Rather, treatments appear to control the pathway along which each axillary primordium develops, within the limits established by the position of the primordium along the long-shoot bud (Fig. 5), and the position of the long-shoot bud within the tree.

It should be borne in mind that any treatment used will be most effective if applied at the normal time of cone-bud differentiation (Fig. 2); and that some time must be allowed for the treatment to have an effect on the sites of cone-bud differentiation within the long-shoot bud. Several treatments, such as various combinations of drought, nitrate fertilizer, girdling, and hormone applications, can have an additive, or synergistic, effect. Results are variable, showing large differences between trees, locations, years, weather, and the specific techniques used. Before any large-scale cone induction trials are begun, original reports should be consulted.

Pollen-Cone Development

Pollen-cone buds resume growth and development usually in April, approximately two months before pollination (Owens *et al.* 1982) (Fig. 2). Pollen cones enlarge slowly for about one month and gradually emerge from their bud scales while the long-shoot bud, on which they are borne, elongates (Fig. 5).

The dormant pollen cone consists of many microsporophylls, each bearing two pollen sacs ("microsporangia") (Figs. 7, 20*A*). Dormant pollen sacs contain sporogenous cells which, after dormancy, divide to form the enlarged pollen mother cells ("PMC") (Fig. 20*B*). Approximately one month after pollen-cone dormancy ends, all microspore mother cells undergo "meiosis" — a special form of cell division that produces four microspores, each with 12 chromosomes, half ("haploid") the original 24. (Fig. 20*C*). During the next month, each microspore develops into a pollen grain (Fig. 20*D-G*).

At first microspores are angular, but soon round out, storing many starch grains and forming a thick wall of two distinct layers. A thick outer layer ("exine"), which has a sculptured outer surface, forms first, followed by a thin, smooth inner layer ("intine"). Early in development the exine separates from the

FIGURE 21. Branch at pollination showing mature brown pollen cones. Needles have begun to burst through short-shoot bud scales. (X 1.5)

intine at two adjacent areas, forming two air-filled wings ("sacci") (Figs. 20*D*, 22).

After sacci form, the single haploid cell divides unequally twice, each time producing a small lens-shaped "prothallial" cell (Figs. 20*E*, *F*). The remaining large cell, or "antheridial initial", then divides unequally again, producing a small "generative" cell and a large "tube" cell. This results in a four-celled pollen grain which is shed within a few days (Figs. 20*G*, 22). Development of the pollen grain resumes after it has been shed and has entered the seed cone. At that time the generative cell divides equally, forming a "stalk" cell and a "body" cell (Fig. 20*H*). The body cell eventually forms two male gametes after a pollen tube has developed.

Mature pollen has distinct sculpturing on the wings and corpus (Fig. 23). Lodgepole pine pollen is small, the body 32-41 μ m long, 33-43 μ m wide, and 14-23 μ m high. The pollen, including wings which are slightly pendulous over the body, is 42-49 μ m wide.

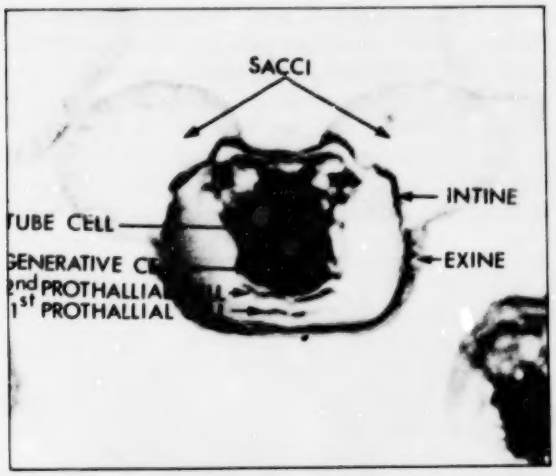


FIGURE 22. Section of a mature 4-celled pollen grain. (X 1100)

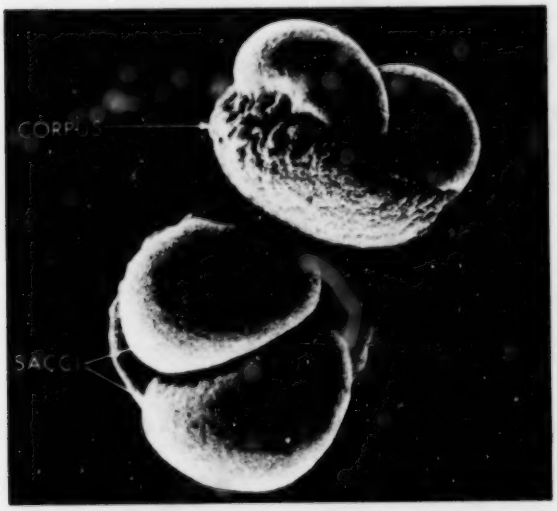


FIGURE 23. Scanning electron micrograph of mature pollen showing the two sacci attached to the corpus and the sculpturing on the exine. (X 870)

No consistent differences occur between the pollen of lodgepole and shore pines.

As the pollen matures pollen cones turn from green to yellow, and then to brown (Fig. 21) as they dry. Each pollen sac then splits open releasing the pollen. Contained in each pollen cone are about half a million pollen grains. The mature, yellow pollen is dry, very small and light, and is carried by wind to the receptive seed cones. Because dry, empty pollen cones may be retained on the tree for many months, quantities of good pollen can be obtained if cones are collected after they have begun to turn from yellow to brown, just before they begin to shed (Fig. 21). Pollen cones collected too early will not open completely and any pollen they yield will likely be inviable.

The rate of pollen-cone development is rapid during warm weather and slow during cool or rainy weather. Consequently, much variation in the time of pollen shedding exists between trees, varying by year and area.

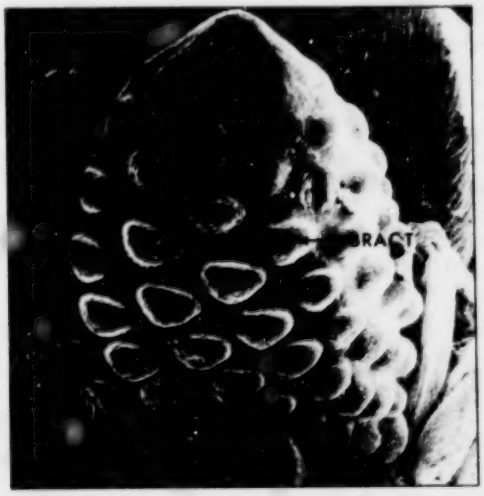


FIGURE 24. Scanning electron micrograph of a dormant seed-cone bud. (X 40)

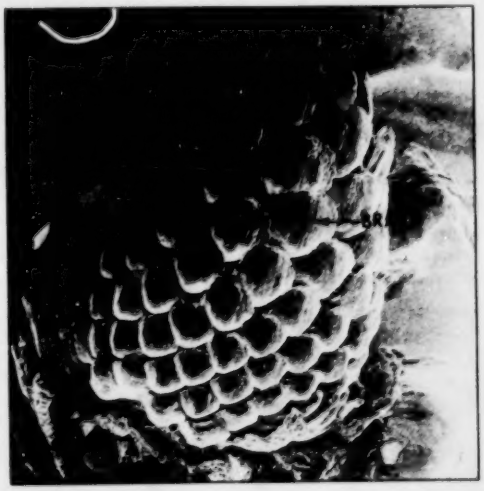


FIGURE 25. Scanning electron micrograph of a seed-cone bud collected five weeks after dormancy ended. (X 25)

Seed-Cone Development

Seed-cone buds, like pollen-cone buds, resume growth usually in April, approximately two months before pollination. Most seed-cone buds form only about two-thirds of their bracts, and none of their ovuliferous scales, before dormancy (Figs. 5*F*, 9, 24). When they resume growth they form the remaining bracts rapidly (Fig. 25), and above each bract, a

broad, axillary ovuliferous scale is initiated (Fig. 26). Lodgepole pine seed cones form about 120 bracts, each with an axillary ovuliferous scale. However, only about 25 of the distal ovuliferous scales develop fully (Fig. 27) and bear two functional ovules, each of which may develop into a seed. Below this region ovules are initiated, but these remain rudimentary on otherwise normal ovuliferous scales. In a region at the base of the cone ovuliferous scales are smaller and form no ovules. The seed cone is narrow in this sterile, basal region, but broad in the fertile, distal region. At pollination only the fertile portion of the cone is exposed; the rest remains covered by bud scales (Fig. 28).

FIGURE 26. Scanning electron micrograph of the tip of a developing seed-cone bud collected seven weeks after dormancy ended. Shown are the apical meristem (A), the bract, and the initiation of ovuliferous scales (OS). (X 80)

FIGURE 27. Scanning electron micrograph of a seed-cone bud showing the elongating spine of the ovuliferous scales. (X 25)

During the month before pollination, each fertile ovuliferous scale forms two ovules on its upper surface (Fig. 26). At the lower end of each ovule, toward the cone axis, a ring of tissue forms and elongates, forming a long hollow neck with two long arms and an opening ("micropyle") between the arms (Fig. 29). Cells covering the surface of the ovule and the arms secrete many minute droplets which bead on

FIGURE 28. Seed cones at pollination. (X 25)

FIGURE 29. Ovule before pollination drop formation showing the two arms with pollen adhering. Droplets form tiny beads on the surface of the ovule and arms. (X 100)

the surface (Fig. 30), making it sticky so pollen will adhere. These droplets, visible only when viewed

with the scanning electron miscroscope, precede, and are much smaller than, pollination drops. The hollow neck of the integument forms the long, curved micropylar canal at the base of which occurs the "nucellus". A shallow depression, or "pollen chamber", forms in the tip of the nucellus (Fig. 39).

Pollination

Approximately two weeks after cone-bud dormancy ends, seed-cone buds begin to protrude out from the long-shoot bud (Fig. 2). During the next month, seed-cone buds enlarge rapidly, and one to two weeks before pollination they begin to emerge through the bud scales (Fig. 33). The distal, fertile ovuliferous scales emerge completely from the bud scales to form a pink to red rosette (Fig. 34). During the next two to three days the cone axis elongates and separates the ovuliferous scales (Fig. 35), exposing the cream-coloured bracts and ovules (Fig. 36). This allows

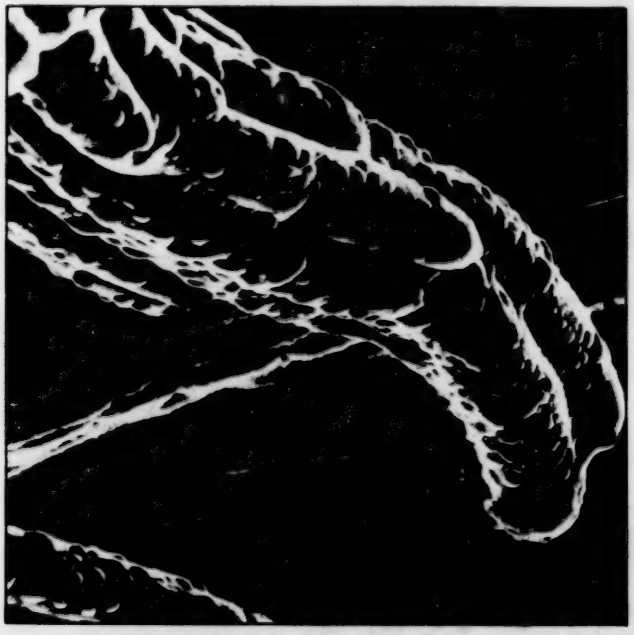


FIGURE 30. Enlarged view of Figure 29 showing tiny droplets on the micropylar arm. (X 500)

pollen to sift down to the ovules where it adheres to all surfaces (Fig. 29).

Within another two to three days, large pollination drops begin to exude out of the micropyle of some of the ovules (Fig. 31). The proportion of ovules exuding pollination drops at any one time varies between cones and trees. Pollination drops are visible within a cone for two to four days and appear to be exuded from the nucellar tip of each ovule. A higher proportion of ovules have pollination drops during periods of rain or high humidity. Pollination drops are also more abundant early in the morning than later in the day. When humidity is low and water stress within the tree is high, most pollination drops are withdrawn into the micropyle (Lill and Sweet 1977; Owens *et al.* 1981). Because pollination drops are large, filling the space between the arms and often completely covering the arms and part of the ovules (Fig. 31), they pick up pollen adhered there. Pollen is, consequently, withdrawn into the micropyle with the pollination drop (Fig. 32). (Pollen landing on a pollination drop apparently causes the drop to be withdrawn.) It is not known of lodgepole pine how many times an ovule can exude a pollination drop or if, once pollen has been taken into the ovule, another pollination drop can be exuded.

FIGURE 31. Ovule at pollination showing a large pollen drop (PD) covering the arms and adhering to the adjacent ovuliferous scale. (X 100)

FIGURE 32. Ovule with pollination drop (PD) being withdrawn. (X 80)

Once pollination drops are no longer exuded, the ovuliferous scales thicken (Fig. 37) and within one week seal the cone (Fig. 38). After the pollination drops are withdrawn the arms on the ovules wither and the cells lining the micropylar canal divide and enlarge, forming a collar that seals the pollen within the ovule (Fig. 40).

Pollination drops are slightly more viscous than water and contain low concentrations of several sugars (McWilliam 1958). At pollination, ovules are oriented with the micropyle sloping down (Fig. 29). Pollen entering a pollination drop floats upward in the drop, usually with the wings pointed downward, and generally settles in the pollen chamber of the nucellus (Fig. 39). Cells at the tip of the nucellus break down and the pollen sinks deeper into the nucellus where it germinates. Each pollen grain forms a pollen tube which grows about half way through the nucellus (Fig. 40) before the seed cone becomes dormant in mid-summer (Fig. 41).

The optimal time for pollination, in order for the maximum amount of pollen to enter the micropyle, can be estimated from observations of cone development (Owens *et al.* 1981). At least six stages can be recognized, varying in their degree of receptivity (Figs. 33-38). At stage 1 the seed cone has just begun to emerge from the bud scales (Fig. 33); at stage 2 the tip of the cone has emerged to form a pink to red rosette (Fig. 34); and at stage 3 most of the cone has emerged from the bud scales, but the cone axis has

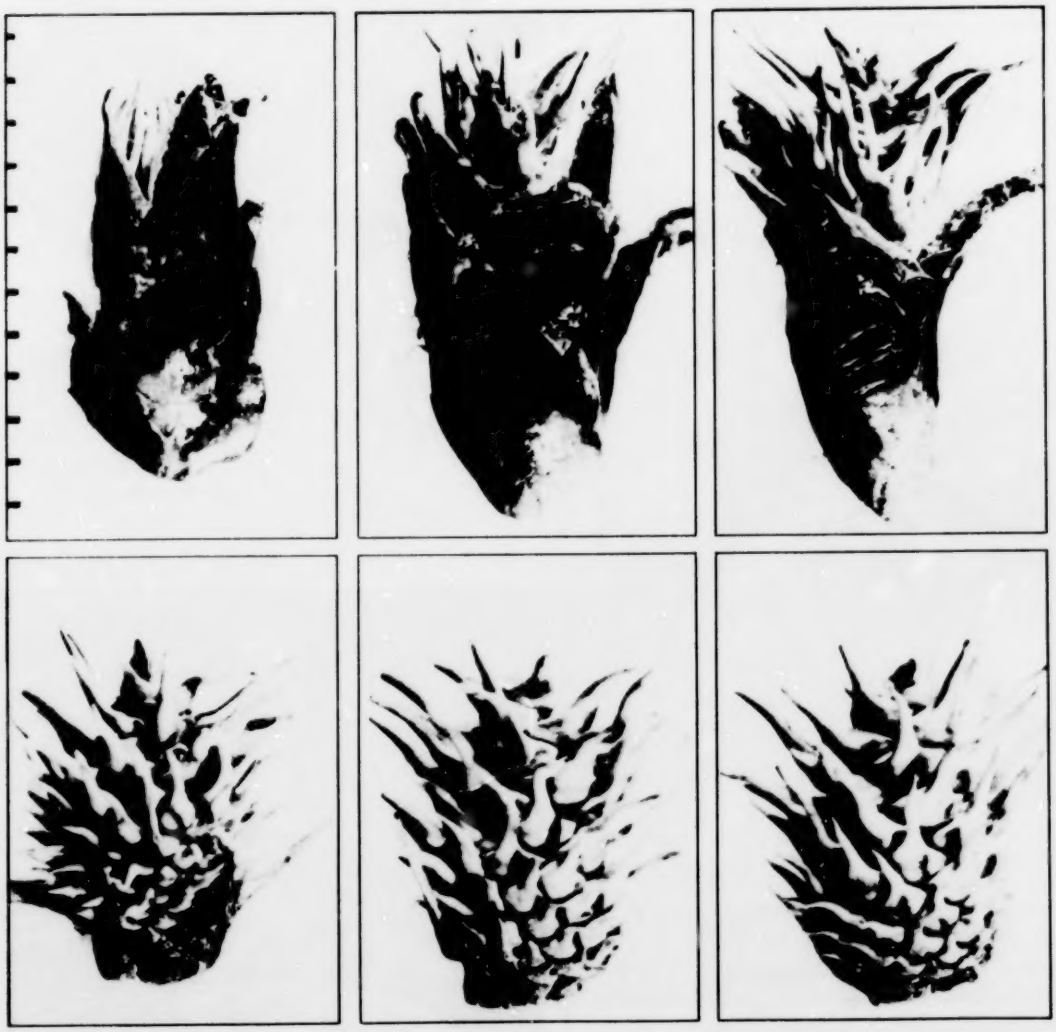


FIGURE 33-38. Stages of seed-cone development and the optimal time for pollination. FIGURE 33. Stage 1. Seed cone starting to emerge. Not receptive. FIGURE 34. Stage 2. Seed cone emerging. Some pollen may reach the ovules. FIGURE 35. Stage 3. Seed cone emerged but no pollination drops have formed. Some pollen may reach the ovules. FIGURE 36. Stage 4. The most receptive stage is when the cone is completely emerged. Pollination drops are present and spaces between the scales allow pollen to sift down to the ovules. FIGURE 37. Stage 5. The scales have begun to thicken, preventing most pollen from entering the cone; few pollination drops are present. FIGURE 38. Stage 6. The cone is sealed and all pollination drops have been withdrawn. The scale in mm is shown on Figure 33.

not elongated enough to leave wide spaces between the scales (Fig. 35). Some pollen landing on the scales during these three stages may sift down between the upper scales, adhere to the sticky surface of the ovules (Fig. 29), and be picked up by the pollination drops later exuded (Fig. 31). If pollination occurs only at these early stages, very few filled seeds result. At stage 4, spaces between the scales open (Fig. 36) and pollination drops form. Although this is the best stage for pollination, cones remain at this stage for only a few days. At stage 5 scales begin to thicken (Fig. 37), restricting some pollen from entering the cone, and most pollination drops have been withdrawn. At stage 6 the scales have thickened to seal the cone and all pollination drops have been withdrawn (Fig. 38). Some filled seeds may result from pollinations made at stage 5, but none will result from pollen applied at stage 6.

FIGURE 39. Section of an ovule at pollination showing a pollen grain settling into the depression (pollen chamber) in the nucellus. (X 150)

Even if large amounts of pollen are applied to the seed cone of lodgepole pine at the optimal time for pollination, the maximum number of pollen grains to be taken into the ovule is only about three, with the average number being two (Owens *et al.* 1981). The small amount of pollen taken in may result from a combination of the short period of cone receptivity, the ephemeral nature of the pollination drop, and the small size of the micropylar canal.

In lodgepole pine, as in other pines (Sarvas 1962, Lill and Sweet 1977), if no pollen enters the ovule, the ovule will abort during summer (Fig. 41). If many ovules abort, the entire seed cone will abort during that summer or autumn and may drop from the branch. During spring and summer pollinated seed cones enlarge and bend downward to a horizontal position. They become dormant in August and retain this appearance until dormancy ends the next spring (Fig. 42).

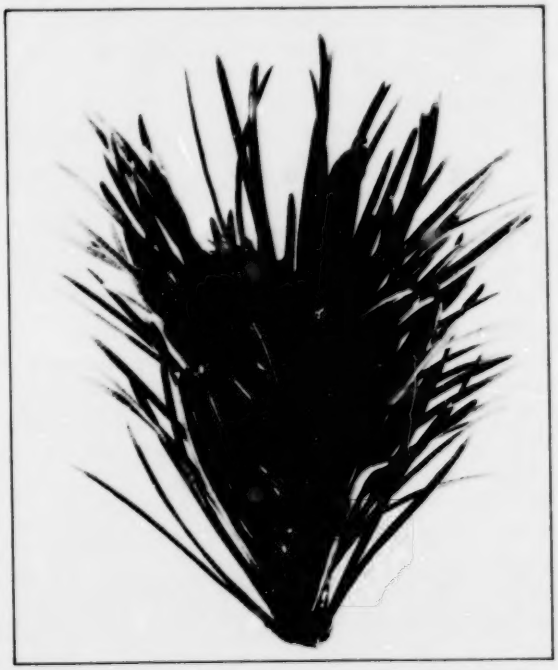


FIGURE 42. Branch bearing a dormant seed cone six months after pollination. (X 1)

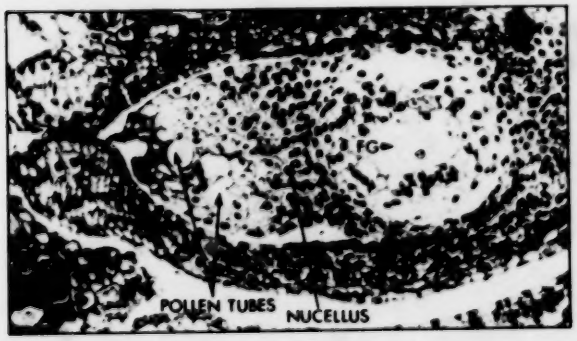


FIGURE 40. Section of a pollinated ovule from a dormant seed cone collected four months after pollination. Micropyle (M) is sealed, pollen tubes are present, and the female gametophyte (FG) is at the free nuclear stage. (X 130)

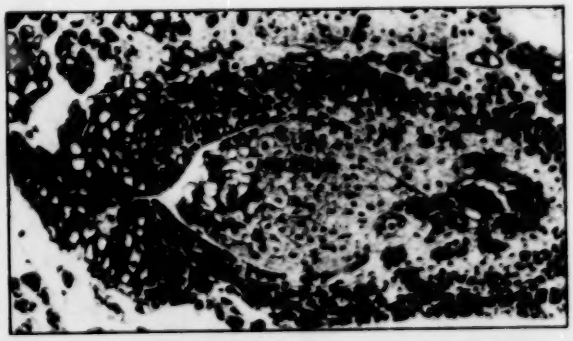


FIGURE 41. Section of an unpollinated ovule at the same time as shown in Figure 40. No pollen is present. Cells in the nucellar depression and in the centre of the ovule have degenerated. (X 130)

Pre-Dormancy Ovule Development

During pollination the ovules enlarge and a single, large megaspore mother cell forms in the centre of the nucellus ("megasporangium") (Fig. 43*B*). Just after pollination, the megaspore mother cell divides by meiosis, forming four megaspores, each haploid, with 12 chromosomes rather than the original 24 (Fig. 43*C*). The outer three megaspores degenerate while the inner, functional megaspore enlarges (Fig. 43*D*) and undergoes a sequence of nuclear divisions which form a large sac-like structure containing many nuclei (Fig. 43*E*). This free nuclear stage of development is reached by mid-summer, at which time the seed cone stops development and becomes dormant (Owens *et al.* 1981) (Figs. 2, 40, 42). Ovules that are not pollinated, or do not contain viable pollen, abort before the cone becomes dormant (Fig. 41).

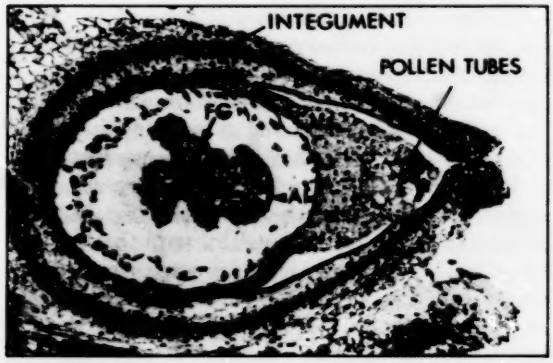


FIGURE 44. Median section of an ovule after dormancy, showing the integument layers, pollen tubes within the nucellus, and the cellular female gametophyte (FG) with an archegonial initial (AI). (X 60)

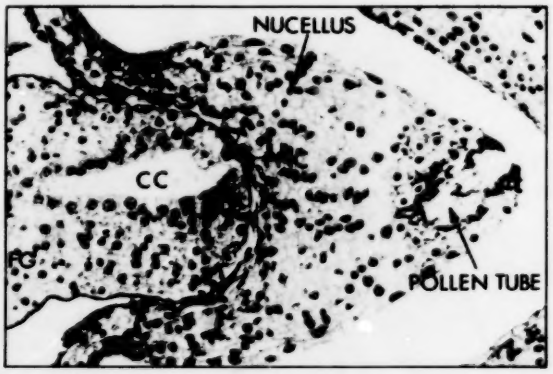


FIGURE 45. Median section of an ovule showing the pollen tube in the nucellus, and the female gametophyte (FG) in which the large central cell (CC) and small primary neck cell (PNC) have formed the archegonial initial. (X 100)

Post-Dormancy Seed-Cone Development

Seed cones resume development in early April (Owens *et al.* 1982). They enlarge rapidly, the ovules growing to their maximum size by the end of May (Fig. 2). The ovule consists of an integument, or ovule wall, enclosing a nucellus (Fig. 43). During April and May the small, free nuclear female gametophyte which wintered over, forms several hundred free nuclei. Cell walls then form, separating the female gametophyte into many haploid cells (Fig. 43*F*). Most of these cells divide, but several at the micropylar end enlarge and function as archegonial initials (Figs. 43*F*, 44). In May, each archegonial initial divides unequally, forming a small primary neck cell on the surface of the

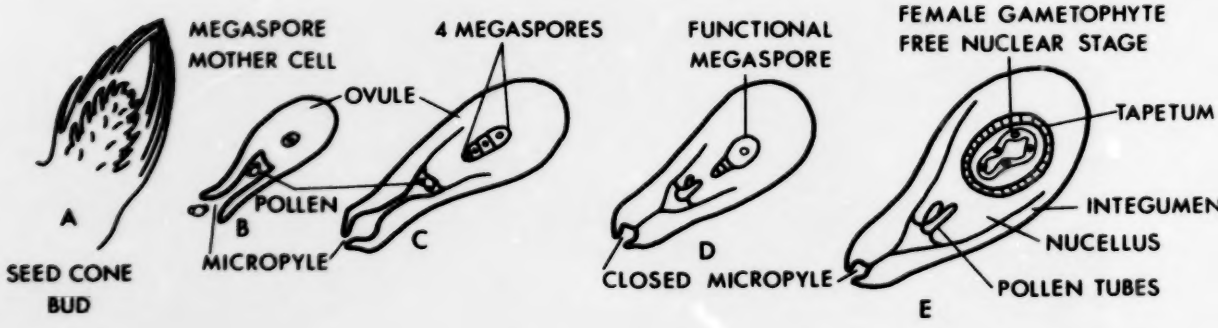


FIGURE 43. Ovule and female gametophyte development. *A*. The dormant seed-cone bud. *B - H*. Ovule development. *B - E*. Predormancy development. *F - H*. Postdormancy development.

female gametophyte, and a large central cell on the inside (Figs. 43*G*, 45). Each primary neck cell divides, forming a single layer of neck cells that become recessed in the surface of the female gametophyte (Fig. 47). The central cell enlarges, develops vacuoles, and begins to store food in the form of lipoprotein within the vacuoles. Around the central cell many small cells form a single-layered archegonial jacket (Fig. 43*G*). In late May the central cell divides unequally, forming a small ventral-canal cell below the neck cells, and a large egg cell (Fig. 43H). This mature female gametophyte (Fig. 46), developed before fertilization, contains two to three archegonia, and is enclosed by a thin megaspore cell wall.

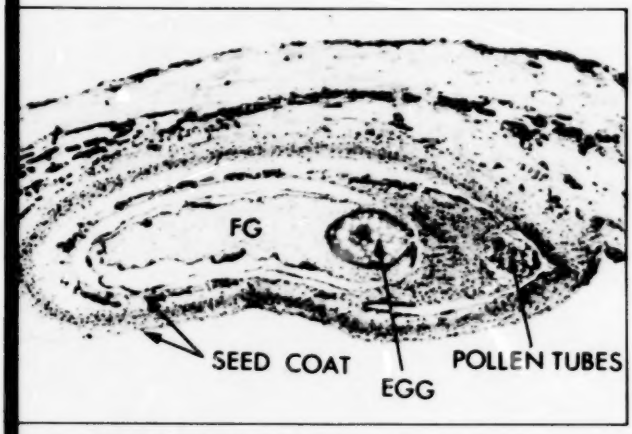


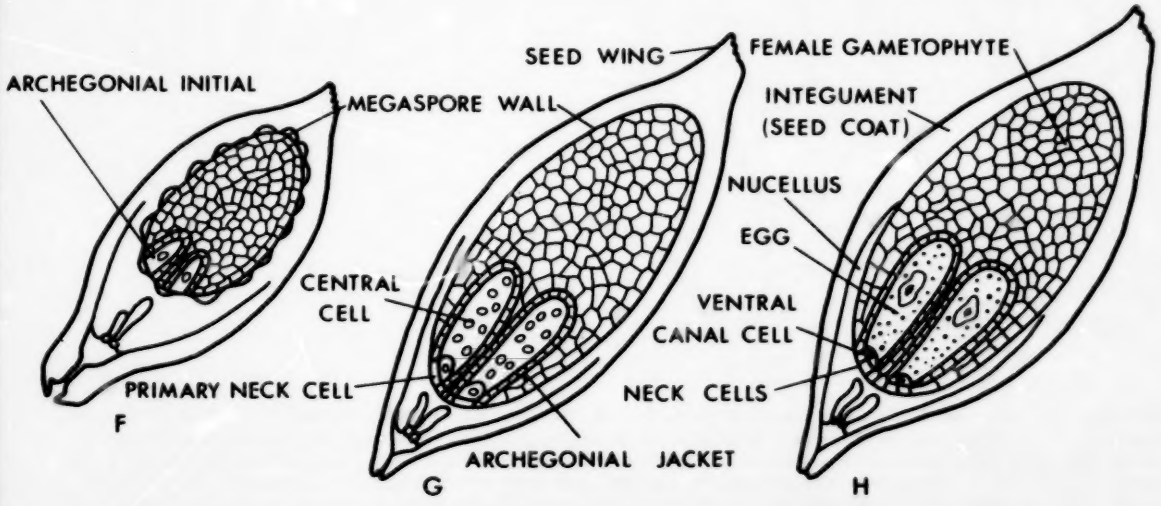
FIGURE 46. Median section of an ovule on the ovuliferous scale just before fertilization, showing the large egg cell within the female gametophyte (FG). (X 40)

One male gamete, generally the larger, passes directly to the egg nucleus. Fertilization is complete when the male gamete fuses with the egg nucleus (Figs. 48, 49*A*), usually in early June (Fig. 2). This re-establishes the full complement of 24 chromosomes in the fertilized egg, or "zygote". The second male gamete, as well as other cells from the pollen tube, have no function within the archegonium and soon degenerate. If none of the eggs within an ovule become fertilized, the female gametophyte also degenerates. The resulting seed contains only shrivelled contents and the seed is not viable.

FIGURE 47. Pollen tubes growing through the nucellus. Above the central cell (CC) a single layer of neck cells (NC) lies in a slight depression formed in the female gametophyte (FG). Tapetal cells (T) fill the depression. (X 150)

Fertilization

As the female gametophyte develops during April and May, the pollen tubes resume growth through the nucellus (Owens *et al.* 1982) (Fig. 47), each tube growing to a separate archegonium. The body cell from the pollen grain is carried along within the pollen tube. When the pollen tube reaches the archegonium, the body cell divides, forming two nearly equal-sized



male gametes. The pollen tube penetrates the neck cells, bursts, and discharges its contents into the large egg cytoplasm (Fig. 49*A*).

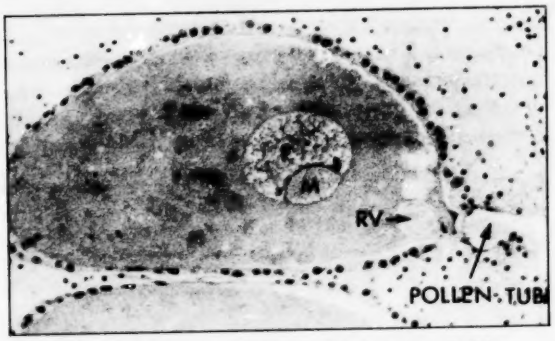


FIGURE 48. Fertilization. The pollen tube has penetrated the neck cells releasing its contents into the receptive vacuole (RV) in the egg cytoplasm. The male (M) and female (F) nuclei are fusing. (X 250)

The Embryo

Pines undergo an elaborate proembryo stage followed by embryo development (Singh 1978) (Fig. 49). Proembryo development in lodgepole pine (Owens *et al.* 1982) begins in early June and continues during the next 10 weeks (Fig. 2). Development occurs entirely within the female gametophyte tissue, which serves as the stored food for the developing embryo.

Proembryo development commences when the fertilized egg nucleus divides into two (Fig. 49*A*), then four, nuclei contained in a dense region of "neocytoplasm" in the centre of the egg cell. The neocytoplasm and the four nuclei migrate to the end of the egg cell opposite the neck cells (Fig. 50). The nuclei become oriented into a single tier (Fig. 49*B*), and each nucleus divides. Cell walls form between the eight nuclei to create two tiers of four cells each (Fig. 49*C*). Each cell divides again, forming a 16-celled proembryo consisting of four tiers of four cells each (Fig. 49*D*). The proximal "open tier" remains receptive to the egg cytoplasm and apparently functions to absorb nutrients stored in the egg cytoplasm. The adjacent "rosette tier" has no known function, but may divide and form small clumps of cells — often mistakenly called "rosette embryos". The next tier of cells, the "suspensor tier", elongates and thrusts the distal, or "apical tier" out of the archegonial jacket into the female gametophyte tissue (Fig. 49*E*). Cells of the apical tier divide, forming distal apical cells and embryonic tube cells. The latter elongate and

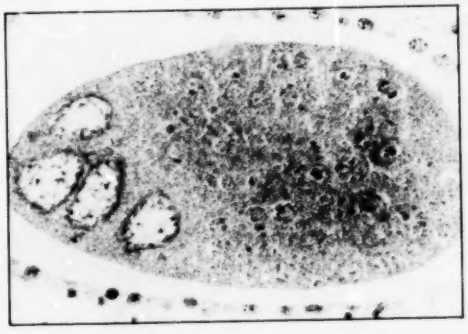


FIGURE 50. Four free nuclei of the proembryo after migrating to the distal end of the archegonium. (X 300)

force the apical cells still further into the female gametophyte (Fig. 49*F*).

The archegonia collapse as their stored food is depleted, and a small corrosion cavity forms in the

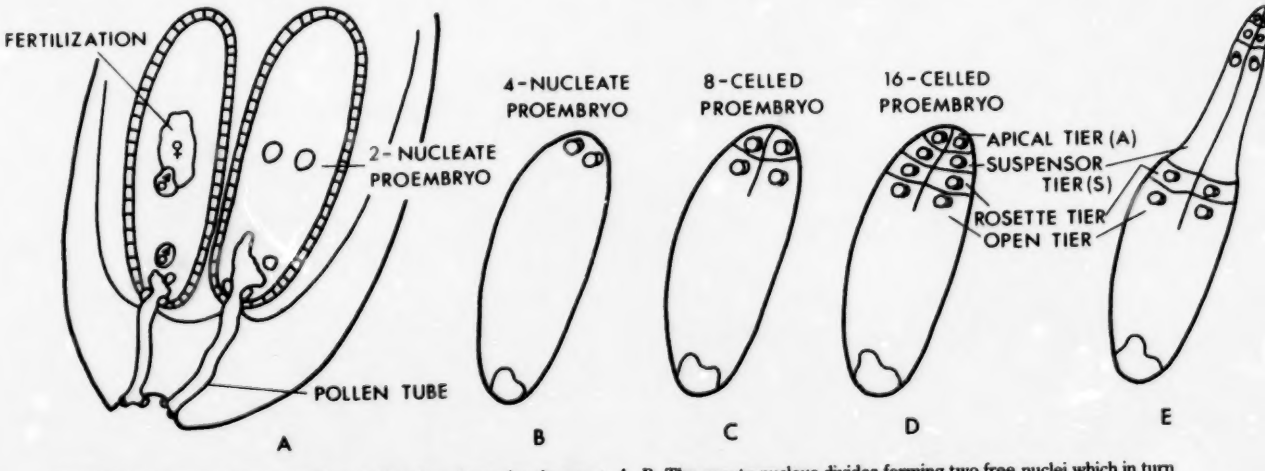


FIGURE 49. Fertilization, proembryo and early embryo development. *A, B.* The zygote nucleus divides forming two free nuclei which in turn divide to form four free nuclei. These nuclei migrate to the distal end of the archegonium. *C, D.* Division and cell formation occur forming the 16-celled proembryo. *E.* The suspensor tier elongates, forcing the apical tier into the female gametophyte. The apical tier divides to form apical cells and embryonal tubes. *F.* Cleavage polyembryony occurs when the apical cells and embryonal tubes (e^1, e^2) separate and form four files of cells. *G, H.* Apical cells divide forming multicellular embryos which are pushed further into the female gametophyte by the elongating embryonal tubes and suspensors. Some embryos degenerate.

female gametophyte tissue around the embryo tier and elongating suspensor cells. The corrosion cavity (Fig. 51) results from the breakdown of female gametophyte cells and the subsequent utilization of their stored food by the developing embryo.

Most conifers undergo one or two types of "polyembryony" — the process by which several embryos can develop within one ovule (Singh 1978). In pine two types of polyembryony take place. "Simple polyembryony" occurs when more than one egg is fertilized within an ovule. Lodgepole pine has two to three eggs per ovule and each egg may be fertilized. Potentially each resulting pro-embryo can develop into a mature embryo. Because each proembryo in simple polyembryony results from separate pollen grains, every proembryo is genetically different from the others. Consequently, one proembryo usually is more vigorous and the others degenerate.

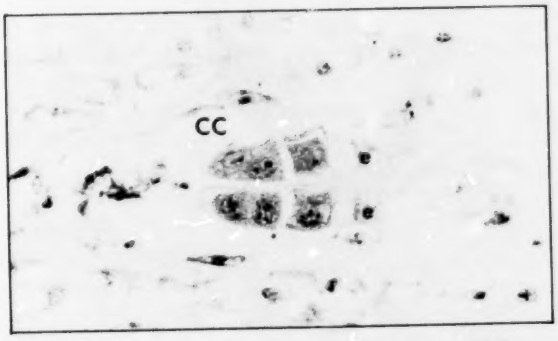
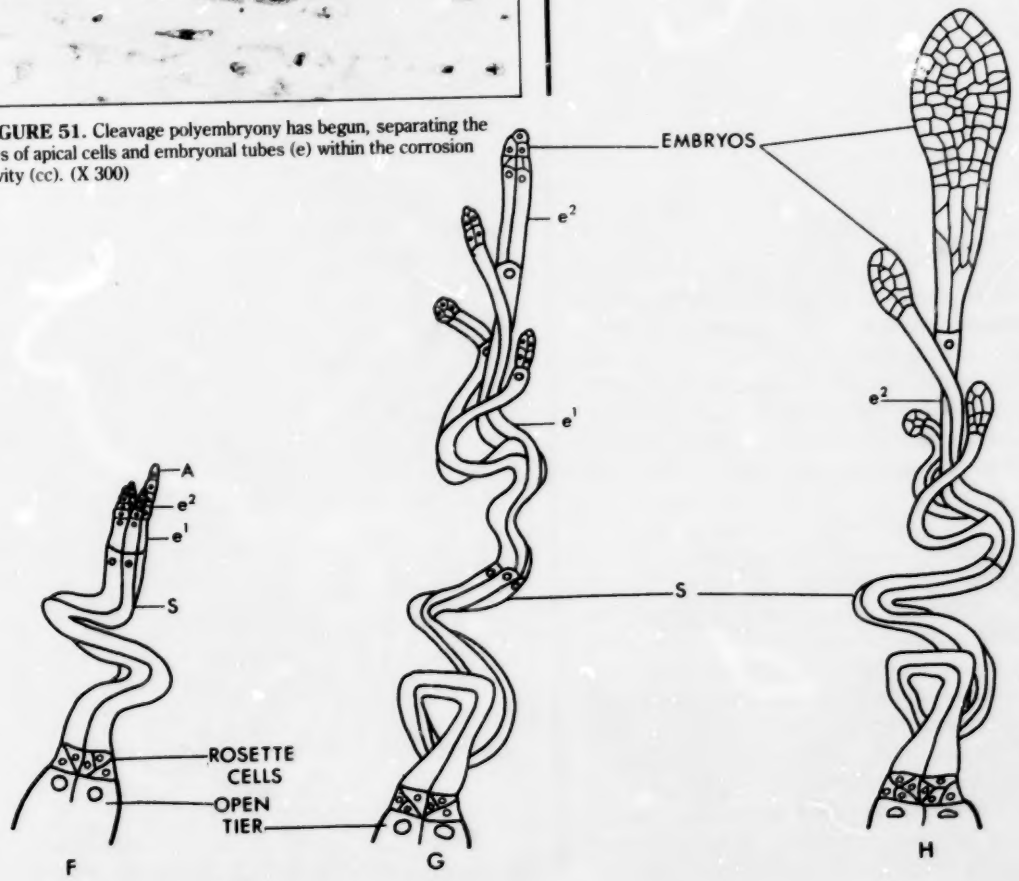


FIGURE 51. Cleavage polyembryony has begun, separating the files of apical cells and embryonal tubes (e) within the corrosion cavity (cc). (X 300)

Pines also undergo "cleavage polyembryony". That is, after the suspensor tier elongates and embryonal tubes form, the apical tier separates into four files of cells (Figs. 49*F*, 51). Each file from one proembryo can develop into a separate, but genetically identical embryo. Again, despite their genetic identity, one of these embryos soon becomes the most vigorous and the other embryos degenerate (Figs. 49*G*, *H*, 52). In a lodgepole pine ovule having three eggs, all of which become fertilized, three proembryos could form by simple polyembryony. In turn, each proembryo could form four embryos by cleavage polyembryony. As a result, 12 young embryos may begin to develop, though a mature seed seldom yields more than a single seedling. All other embryos cease development.

Each apical cell divides many times, forming a small club-shaped embryo at the tip of the coiled suspensor (Fig. 49*H*). The club-shaped embryo that survives the polyembryonic selection process is pushed by the suspensor to the middle of the female gametophyte tissue (Fig. 52). Here, the embryo enlarges rapidly (Fig. 49*H*). Cells at the distal end form several cotyledons around a dome-shaped apex. The root apex forms below the shoot apex, while the more basal cells form a thick suspensor system (Fig. 49*H*).



The axis elongates between the root and shoot apices, and a long root tip forms before the embryo becomes mature and dormant in mid-August (Fig. 53).

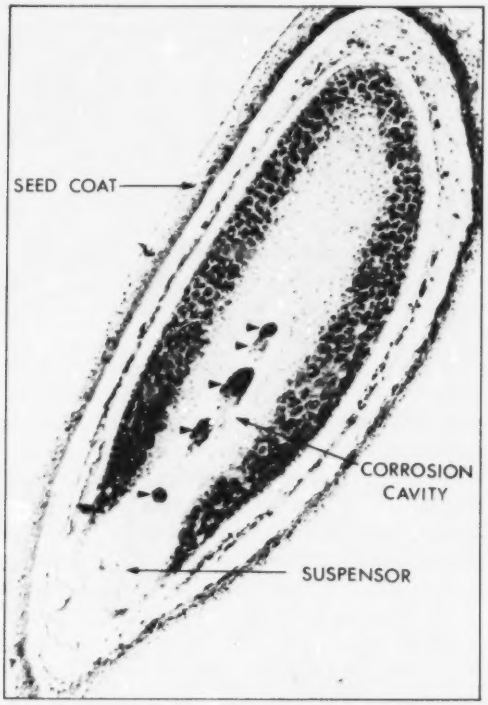


FIGURE 52. Five multicellular embryos (arrowheads) resulting from simple and cleavage polyembryony at the end of the coiled suspensor. The corrosion cavity is present and the seed coat is differentiating. (X 35)

The Seed

Even before fertilization the seed coat, or "testa", begins to differentiate from the integument (Fig. 46). The integument forms three distinct layers characteristic of most conifer seeds: (1) the thin, dark outer layer, which is fused with the seed wing; (2) the thick, hard, stony middle layer; and (3) the thin inner layer, which lies adjacent to the nucellus.

Seed wings begin to differentiate after winter dormancy. A seed wing develops from the outer cell layers of the ovuliferous scale that remain fused to the ovule. Before fertilization a layer of cells forms under the ovule and seed wing. This cell layer degenerates, allowing the seed and seed wing to separate from the ovuliferous scale at about the time of fertilization.

In the mature seed, the embryo is loosely packed within the rather firm, white, nutritive female gametophytic tissue, often called "endosperm" (Figs. 53, 54). This tissue contains abundant stored food and functions as a food reserve for the developing embryo and the young, germinating seedling. A thin megaspore wall encloses the entire female gametophyte. The brown nucellus is thick and conspicuous only at the micropylar end of the seed (Owens *et al.* 1982).

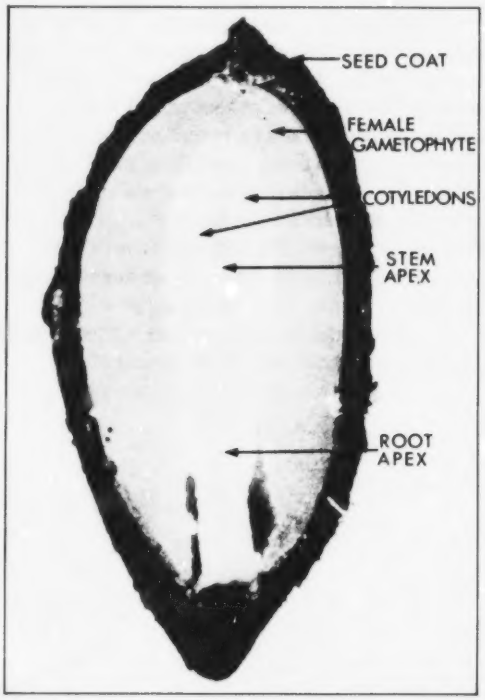


FIGURE 53. Dissected, dewinged, mature seed. (X 28)

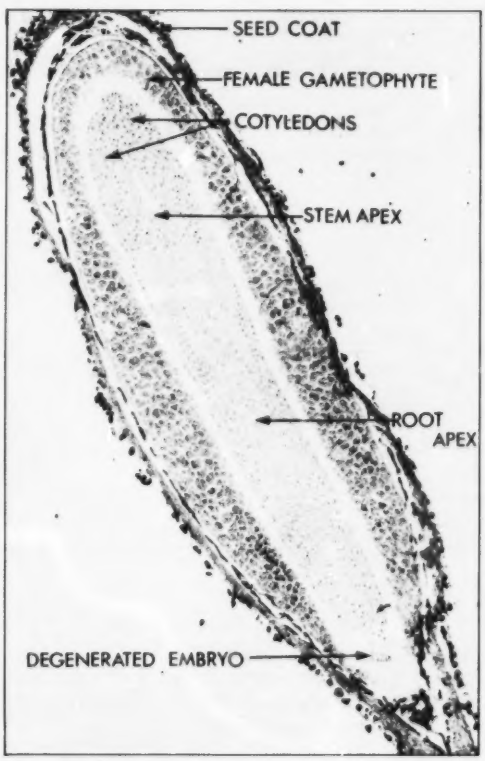


FIGURE 54. Median section of a mature seed. (X 35)

Cone Maturation, Seed Release, and Regeneration

Just over two years elapse between the initiation of seed cones and the attainment of maturity by the seeds (Owens *et al.* 1981, 1982). Approximately 17 months elapse between pollination and seed maturity (Fig. 2). The seed cones are elongated fully when ovules become fertilized in June of the year following pollination. The months of July and August show little external change in appearance of the seed cone (Fig. 55). Internally, however, embryos and seeds develop rapidly and the scales of the seed cone become hard and woody.

When shore pine seed cones are mature they begin to dry and the scales begin to separate, opening the cone (Fig. 3). Dry weather at this time will cause more rapid drying, and earlier opening, of the cone, with faster release of the seeds. Most seed is released from the mature cones in fall, although wet weather may cause the scales to swell, closing the cones periodically. Mature but empty seed cones may remain on the tree for several years.

Seed cones of lodgepole pine (Fig. 55) are usually serotinous. That is, the scales are stuck together firmly by resin, often requiring extreme heat (45-50°C) and drying before they will separate, opening the cone. In the absence of such heat, cones may remain closed for several years. Serotiny is not as extreme in lodgepole pine as in some other pines, where cones may remain closed for many years. Also, considerable variation in the degree of serotiny exists between individual trees in the same stand (Lotan 1975).

Seeds may remain viable for several years within sealed serotinous cones. In a mature stand of lodgepole pine, millions of seeds per hectare may be stored within the closed cones. As in other serotinous pines, the amount of seed available for regeneration in a stand is a consequence of accumulative production over several years, rather than of annual production - as in non-serotinous conifers (Lotan 1975). The heat generated from a forest fire causes the cones to open and release large numbers of seed at one time. In addition, fire removes much of the litter on the forest floor, changes soil nutrient levels, and reduces shade cover and competition, thus providing a good seed-bed for rapid regeneration. The abundant seeding that follows a fire and the rapid growth of young lodgepole pine often result in stands of uniform age (Baumgartner (editor) 1975).

Lodgepole pine, over much of its range, exists in a fire-dependent ecosystem where succession by other climax species is frequently interrupted by fire. Many lodgepole pine forests have been perpetuated by repeated fires. If fire is excluded, a viable lodgepole pine ecosystem may not be maintained (Lotan 1975).

FIGURE 55. Mature seed cone of lodgepole pine. (X 1.5)

Seed Extraction, Storage and Germination

For seed extraction in lodgepole pine it is recommended to kiln dry the cones for 18 hours at 60°C. Higher temperatures may cause cones to open more rapidly, but may also result in a marked decrease in total seed germination. Temperatures for non-serotinous cones are lower, about 42°C for 13 hours. Complete opening of serotinous cones may be obtained by immersing cones in hot water (60°C) for five to 10 minutes, followed by drying at room temperature. This method works well for small batches of cones (Lotan 1975).

Cleaning of seeds and removal of seed wings (Fig. 56) must be done carefully so that the seed coat is not damaged, thus greatly reducing the viability and storage life of the seed. *Pinus contorta* seed may be

FIGURE 56. De-winged lodgepole pine seed. (X 8)

stored in airtight bags at -19°C, with a moisture content of 6 to 9 percent. Like this it will keep for many years without a significant decrease in viability.[1]

Germination is best if a seed is soaked for 24 hours in water, its surface dried and stratified at 2° for 28 days, and it then be incubated at 20-30°C for 8-hour days and 16-hour nights[2]. Nursery germination normally occurs two to three weeks after sowing. The embryonic root (or "radicle") elongates, ruptures the seed coat, and emerges before the embryonic shoots, or "epicotyl". The embryonic leaves, or "cotyledons", elongate rapidly and become green.

The Seedling

Following germination the stem apex, located between the cotyledons, begins a period of free growth during which primordia are rapidly initiated as the shoot axis elongates. During the first year of growth, seedling shoot development differs from shoot growth in subsequent years. The primordia initiated following germination develop into primary leaves rather than cataphylls. Buds may be initiated in the axils of some of these primary leaves, and these axillary buds develop into short shoots or undergo a period of free growth similar to that in the terminal shoot (Fig. 57). After many primary leaves have

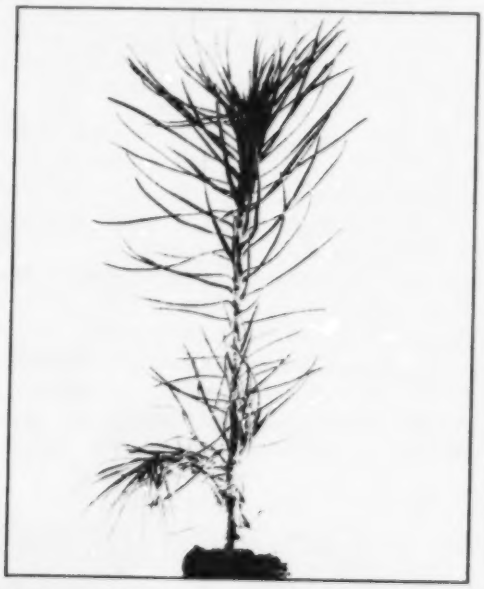


FIGURE 57. One-year old lodgepole pine seedling, reared in a container greenhouse, showing the primary needles. (X 0.75)

formed and the shoot has elongated several centimetres, the primordia, initiated by terminal and lateral apices, develop into small, scale-like cataphylls rather than leaves. This begins the formation of a long-shoot bud which develops in the same manner as on older trees: a series of cataphylls form and short-shoot buds develop in the axils of some of these cataphylls. Axillary long-shoot primordia also may be initiated, followed by a series of sterile cataphylls that enclose the apex and function as bud scales. In autumn the small terminal long-shoot bud becomes dormant. It consists of a preformed, telescoped shoot which will elongate after winter dormancy. The period of free growth, and thus the ultimate height of the first-year seedling, may be increased by maintaining seedlings under long days.

Seed Production

Cone production in *Pinus contorta* is not as cyclic as it is in many other conifers. Although it produces only a few seeds per cone, it commonly produces abundant cones, and good seed crops occur at one to three year intervals. The first seed cones may appear on trees as young as five years old, and the resulting filled seed is just as viable as that from older trees (Fowells (compiler) 1975). Consequently, the total seed production potential for *P. contorta* during the lifetime of a single tree is high. It is not uncommon for mature trees to produce many thousands of seeds per year despite the fact that relatively few seeds may be produced per cone (Lotan 1975).

The seeds, small with small seed wings, are relatively heavy and disseminate only short distances. One kilogram of lodgepole pine seed contains approximately 225 000 seeds, whereas a kilogram of shore pine seed contains approximately 300 000 seeds (Fowells (compiler) 1965). In still air, seeds fall at an average rate of 0.8 metres per second, and most seeds are scattered to distances within 50 to 90 metres from the base of the tree. A few seeds may be disseminated further by birds and squirrels. Seeds may disseminate throughout the year, but not at a uniform rate. Most seeds are shed in the fall and small amounts during the winter (Lotan 1975). Most viable seeds germinate in the spring following dispersal, but a small number may germinate a year later. Best seedling establishment occurs in full sunlight on mineral soil or disturbed duff, free of competing vegetation.

The low average number of filled seeds per cone results from several causes. Most important is that only about 25 of the average 120 ovuliferous scales bear fertile ovules. The basal two-thirds of the cone is sterile. For the approximately 50 fertile ovules within the cone, viable pollen is necessary for normal ovule development. Unpollinated ovules, or ovules pollinated with inviable or incompatible pollen, abort during the summer of the year in which the cones were

[1] and [2] British Columbia Ministry of Forests, Seed Centre, personal communication, 1983, Duncan, B.C.

pollinated. This results in small, flattened, empty seeds. If many ovules are not pollinated in a cone, that cone will abort and often drop from the branch.

Pollinated ovules can develop into viable seeds or inviable seeds whose contents have degenerated. The latter may occur because the eggs were not fertilized even though pollen tubes were present; or because the embryo aborted, or its development was arrested. These varied causes result in normal appearing, but inviable seeds which, when dissected, usually contain a shrivelled female gametophyte or a poorly developed embryo. They generally weigh less than filled seed, and most are removed from commercial seed lots in the separation process.

The pollination mechanism is a weak link in the long chain of events leading to viable seed in *P. contorta*. The seed cones are open and receptive for only a few days during which pollination drops must be present to draw the pollen into the ovules. Extremely dry weather can prevent pollination-drop formation, and extremely wet weather at pollination may flood the cones and prevent pollen from reaching the ovules. Wind direction is also important because *P. contorta* often grows where there are prevailing winds — which blow, ideally from the direction of the pollen source. This may result in one side of the cone or the tree being poorly pollinated.

Summary

The reproductive cycle of *Pinus contorta* is very long, as in all other pines, spanning three growing seasons or about 26 months, from cone initiation in the summer and fall of the first year, to pollination the second year, and fertilization and seed development the third year (Fig. 2). During this time many environmental and physiological factors, not fully understood, can affect development of cones and the development of filled, viable seed. Further understanding of the complete reproductive cycle of *P. contorta* is necessary in promoting and controlling cone and seed production for reforestation.

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